Comparisons Among Growth Characteristics of Two Species of Sea Mussel, *Mytilus edulis* and *Mytilus californianus*

BY

J. R. E. HARGER

Department of Biological Sciences, University of California at Santa Barbara [1]

(11 Text figures; 11 Tables)

INTRODUCTION

THIS PAPER DEALS WITH growth characteristics of two species of sea mussel, *Mytilus edulis* LINNAEUS, 1758 and *Mytilus californianus* CONRAD, 1837, in the waters of Southern California (Santa Barbara).

Mytilus edulis has a world-wide distribution, being present in both northern and southern hemispheres (STUBBINGS, 1954). On the west coast of North America it is commonly found in quiet waters, such as bays, sloughs, etc., but may also occur in considerable numbers on exposed and semi-exposed shores.

Mytilus californianus seems to be endemic to the west coast of North America, with a range extending from the Aleutian Islands to Isla Socorro, Mexico (SOOT-RYEN, 1955). It occurs sparsely within harbors (together with *M. edulis*), but is confined principally to exposed coasts.

Considerable overlap between extremes of exposure and shelter exists in the distribution of the two species and striking examples of populations resulting from this overlap occur on open coast pier pilings in Southern California. Such a situation is found at Ellwood Pier (property of Signal Oil and Gas Company), located some 14 miles west of Santa Barbara on an open sandy shore. Constructed on steel girders, this pier extends approximately ½ mile into the sea, from the shallow surf zone out to a depth of some 40 feet. Intertidal regions of the pilings support enormous clumps of sea mussels consisting of both *Mytilus edulis* and *M. californianus* (HARGER, 1968).

My interest in the biology of these mussels was initially stimulated by the sight of the two species growing together in the same clumps, and, hence, seeming to circumvent the "competitive exclusion principle" (HARDIN, 1960).

Most of the detailed experimental work designed to evaluate the effects of competition between two species of animals having similar ecological requirements have been studies performed in the laboratory. DEBACH (1966) says "almost without exception where two species compete for identical food in the same habitat (laboratory universe), one species displaces the other completely within relatively few generations."

The co-occurrence of large numbers of *Mytilus edulis* and *M. californianus* within the same clump seemed in violation of the above statement, particularly as the limited amount of intertidal piling available for colonization indicated that space must sometimes be limiting to these animals.

The following information relating to growth characteristics of *Mytilus edulis* and *M. californianus* has been gathered as a by-product of experiments originally set up to investigate interactions between the two mussel species.

GENERAL METHODS

Mussels used in the experiments were placed in wire mesh cages suspended intertidally at various heights from the cross-girders at Ellwood Pier or from marina floats in Santa Barbara Harbor. The cages were cylindrical in shape (diameter 7 inches or 7.78 cm, height 8½ inches or 21.5 cm) and constructed from galvanized hardware cloth. Components (wire sections, etc.) used in cage construction were laced together with braided nylon cord and the entire unit was coated with epoxy resin. This coating served to give rigidity to the nylon binding and

[1] Present address: Department of Zoology, University of British Columbia, Vancouver 8, British Columbia.

at the same time to cut down any leaching of zinc ions which might affect enclosed mussels. A log normal distribution of mussel lengths was chosen to represent mature mussel populations, since this was similar to the distribution of *Mytilus californianus* within clumps on Ellwood Pier (Harger, 1968). The mussels used ranged in length from 2.5 cm up to 10 cm (for size classes and frequencies, see Table 1). *Mytilus californianus* individuals occurring within clumps are often much larger than 10 cm, but this tends to be the upper size limit for *M. edulis*. A log normal distribution most accurately mimics that of *M. californianus* in natural clumps (Harger, 1968), and although the distribution of *M. edulis* tends to be normal, or bimodal normal if both juveniles and adults are present, it seemed advisable to use an identical size distribution for both species in order to be sure of eliminating any effects which might arise as the result of size differences.

Table 1

Lognormal distribution used to construct experimental mussel populations. Cages containing both *Mytilus edulis* and *Mytilus californianus* received equal representation to make a total of 90 individuals

Size Class	N
2.5 – 3.5 cm	12
< 3.5 – 5.0 cm	32
< 5.0 – 6.5 cm	24
< 6.5 – 8.0 cm	14
< 8.0 – 10.0 cm	8
Total:	90

Cages containing populations of mature mussels were constructed from ½-inch (1.27 cm) aperture hardware cloth and a total of 90 mussels was placed within each cage (equal numbers of the two species for mixed populations). Individual mussels used in the experiments were marked in the following manner: after drying, a small patch was scoured on the shells with sandpaper, code numbers were written on the roughened surface in white ink, and a small drop of clear epoxy resin was placed over the symbols and allowed to harden overnight.

The maximum length of each animal was recorded in centimeters (accurate to 2 decimal places), between the anterior hinge and the posterior siphon regions at the commencement and conclusion of the experiment. (Mussels were removed from water for approximately 12 to 24 hours for marking, etc., and mortality ranged between 10 and 15% as a result of this process.)

All mussels used in the experiments were taken from clumps at Ellwood Pier no more than one day before marking. Before and immediately after marking the animals were kept in running (non-recirculating) sea water. Laboratory containers were well aerated and mussels spent a maximum of 3 days between removal from the pier clumps and replacement at the pier within experimental cages.

METHODS USED TO RECORD SEASONAL FLUCTUATIONS IN GROWTH

Coe & Fox (1942) and Coe (1945) reported that growth of both *Mytilus californianus* and *M. edulis* fluctuated seasonally at Scripps Pier (La Jolla, Southern California). To monitor similar variations at Santa Barbara two replicate cages containing mixed populations of marked *M. edulis* and *M. californianus* were placed at each location where long term competition experiments were run. These positions were the top, middle, and bottom of the mussel clumps at Ellwood Pier and beneath the marina floats in Santa Barbara Harbor. Growth was recorded from the mussels in these cages throughout the year. From these data the mean growth increment of mussels falling within each of 9 size classes at the beginning of each 2-month time period was calculated. Initially, measurements were made at intervals of one month, later this was increased to 2 months to minimize disturbance effects. Data obtained from the monthly recordings were corrected to the longer interval; but the resulting values are probably higher than they would otherwise have been since the effect of removing mussels from the water and measuring them tends to prevent individuals from inhibiting each other's growth (see later).

METHODS USED IN OBTAINING LONG TERM GROWTH INFORMATION FROM ARTIFICIAL "MATURE" MUSSEL POPULATIONS

To investigate the possible effects of competition between *Mytilus edulis* and *M. californianus* an experiment using a 3-way factorial design was set up involving 2 species, 3 intertidal levels, and 4 treatments. The top intertidal level corresponded to the top of the mussel clumps occurring on Ellwood Pier pilings (Harger, 1968) (about 2 feet or 60 cm below the highest tides), the middle level to the middle of the clumps and the bottom level (just exposed at the lowest tides) to the bottom of the clumps. The 4 treatments consisted of different arrangements of mussels within the cages: Treatment 1 consisted of sur-

rounding one species in the center of the cage by the other species; Treatment 2 the reverse; Treatment 3 consisted of mixing individuals of both species as evenly as possible; and Treatment 4 of *M. edulis* or *M. californianus* alone. This experiment was initiated before I was aware of behavioral differences which exist between the two species (HARGER, 1968). Briefly, *M. edulis* individuals react to pressure imposed upon them by crawling against such pressure, whereas *M. californianus* react slowly or not at all. Thus, the first 3 treatments probably became identical since *M. edulis* tended to arrange itself on outer surfaces of the caged clumps. Only cages containing pure *M. californianus* and pure *M. edulis* (3 replicates each) were run at the mid-intertidal level. All other treatments within the design were replicated 5 times.

An extension of this experiment consisted of setting up 2 replicates of the following 3 treatments: evenly mixed *Mytilus edulis* and *M. californianus;* pure *M. edulis;* and finally, pure *M. californianus* in Santa Barbara Harbor. Cages were here suspended from marina floats in such a way as to be approximately one foot (30 cm) below the water surface at all times.

The complete experiment was started during August, 1965; at Ellwood Pier, 3 of the aforementioned 5 replicates were left in the sea for 6 months before removal (including all the mid-tidal cages) and the remaining 2 replicates were withdrawn after one year.

The first 3 replicates were removed after 6 months because the cages were in danger of being washed off the pier by heavy storms experienced by the area at that time. Rather than risk losing a great part of the experiment I elected to analyze $\frac{3}{5}$ of it at that point (3 cages were lost).

METHODS USED IN OBTAINING GROWTH INFORMATION FROM JUVENILE MUSSEL POPULATIONS

To study the effect of competition between juvenile mussels (1.5 to 2.5 cm long) the following experiment involving 3 treatments, each replicated twice, was set up: a) pure *Mytilus edulis* (200 individuals); b) pure *M. californianus* (200 individuals); c) *M. edulis* mixed evenly with *M. californianus* (100 individuals of each species). In this experiment individual animals were not marked, but all were measured at the start and at each inspection. The cages containing them were plastic kitchen colanders (10 inches or 25.4 cm in diameter) placed face to face and lashed together round the edges. The maximum diameter of holes in the colanders was $\frac{1}{4}$ inch (0.63 cm). All cages were first suspended from Ellwood Pier in October, 1965 at the low intertidal position only. The first 3 inspections were made at intervals of one month. Thereafter, in order to reduce effects of disturbance that might influence the outcome of the experiment, the interval was increased to 2 months for the next 2, and to 4 months for the last 3 inspections. In all, a total of 19 months growth was recorded. A further experiment using juvenile mussels was set up during January, 1966 which was designed to check growth and the effects of competition in both rough and calm water. The 2 locations used for this experiment were Ellwood Pier (rough water) and Santa Barbara Harbor (calm water). The experimental populations (200 individuals) were set up in wire hardware cloth cages ($\frac{1}{4}$ inch or 0.63 cm aperture) and positioned in the same manner as previously reported, at the pier (lowest level) and the harbor. In the harbor the 3 treatments (pure *M. edulis;* pure *M. californianus*; and both in even proportion) were the same as reported for the previous experiment, together with a parallel set at Ellwood Pier. Two additional treatments (*M. edulis* and *M. californianus* mixed in the ratio of 3:1 and the reverse) were also used at the latter site. These were designed to investigate the effect of differing initial proportions of the 2 species on the outcome of the competitive process. A checking interval of 4 months allowed time for undisturbed growth.

RESULTS

SEASONAL GROWTH CHARACTERISTICS OF *Mytilus edulis* AND *Mytilus californianus*

Figures 1, 2, 3, and 4 show the bimonthly growth characteristics for 3 size classes (4 - 5 cm, 5 - 6 cm, 6 - 7 cm) of both species of mussels throughout the period November, 1965 to January, 1967 from the bottom, middle, and top positions at Ellwood Pier and from Santa Barbara Harbor. As individual mussels initially present within the 4 - 5 cm size class grew, they passed through and were recorded within the larger size classes at different times. This method of presenting growth data allows the effect of the increasing size of individual organisms to be eliminated from the seasonal pattern without having to set up separate new populations throughout the year. A complete record of smaller size classes (below 4 cm) was not obtained since most small mussels passed into the larger size classes before the experiment was over. Size classes larger than 6 - 7 cm showed a growth pattern similar to that of the 6 - 7 cm class.

At Ellwood Pier, both *Mytilus edulis* and *M. californianus* in cages set in the low position showed a period of "slow" growth between December, 1965 and March, 1966

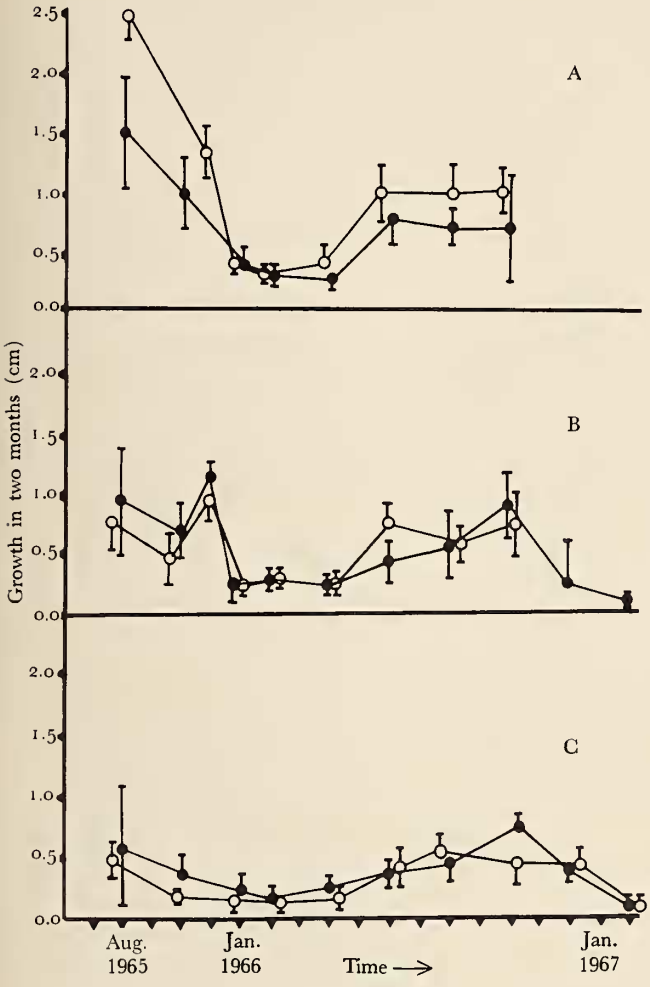

Figure 1

Growth fluctuations for mussels set in cages at the low position, Ellwood Pier (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period August, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

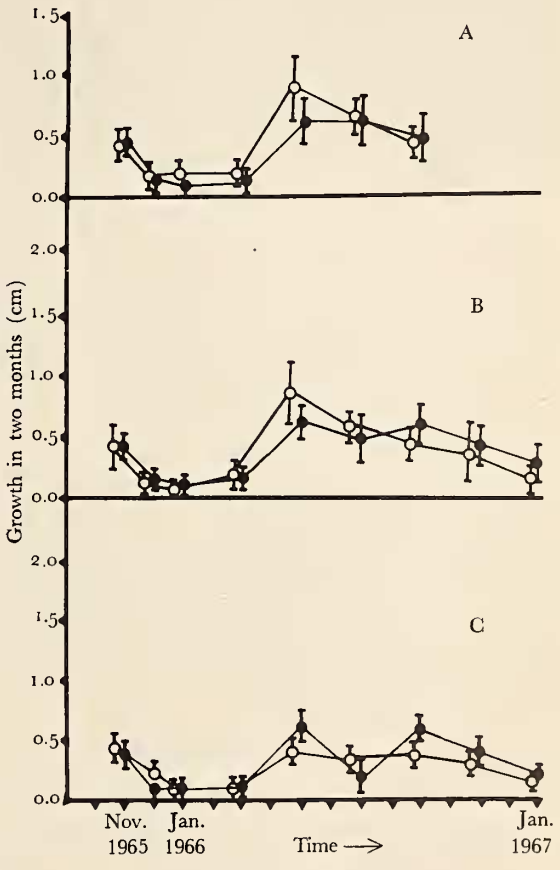

Figure 2

Growth fluctuations for mussels set in cages at the middle position, Ellwood Pier (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period October, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

for all recorded size classes. This was repeated between November, 1966 and January, 1967 (Figure 2). Both periods of slow growth occurred during winter months when water temperature was at its lowest (Figure 5) and when frequent heavy seas occurred, both of which may have limited growth. Maximum growth occurred during the warmer summer months. Similar growth patterns were exhibited by mussels in cages placed in the intertidal region, that is at the middle and the top of the mussel clumps (Figures 2, 3).

In the low cages growth of *Mytilus edulis* within the smaller (4 - 5 cm) class exceeded that of *M. californianus* of the same size class at all times except during the coldest months when both species showed equal growth (Figure 1). In the middle cages, small *M. edulis* individuals grew more than *M. californianus* but only for the first 6 months

of the year, whereas in the upper cages growth of *M. californianus* was always greater than that of *M. edulis*. Growth of the larger *M. californianus* size classes for the most part exceeded that shown by *M. edulis* of similar size except for the 5 - 6 cm size class at the middle and lower levels during the summer months (Figures 1, 2, 3).

In Santa Barbara Harbor, growth of *Mytilus californianus* was lower than that of *M. edulis* for all size classes. Here fluctuations in the seasonal growth pattern for both species were almost non-existent, unlike the situation at Ellwood Pier (Figure 4). This might suggest that it was not low water temperature *per se* that caused low winter growth rates at Ellwood Pier (surface water temperatures were similar in both places throughout the year), but some associated phenomenon such as food scarcity or wave action. Within the harbor wave action was very slight during severe winter storms, whereas the Pier re-

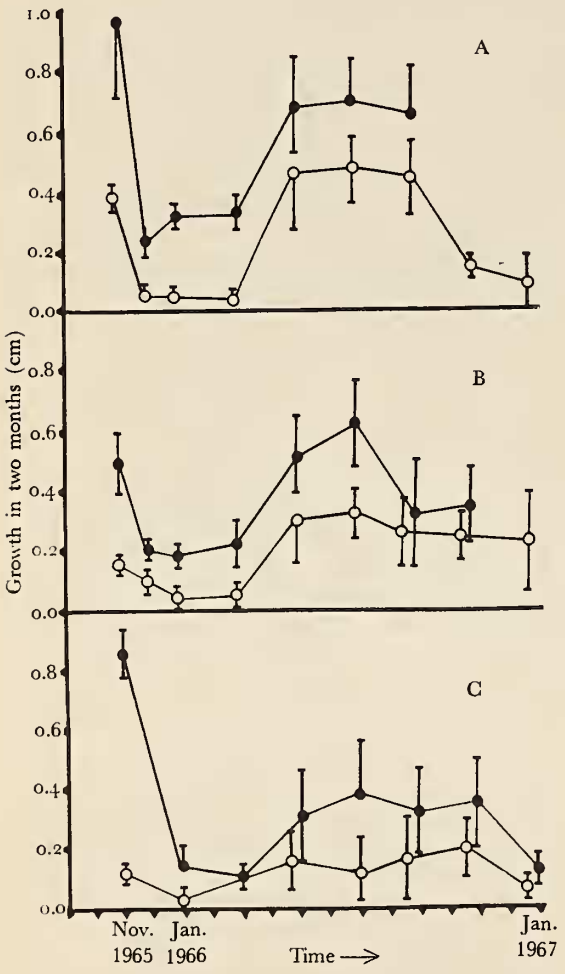

Figure 3

Growth fluctuations for mussels set in cages at the top position, Ellwood Pier (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period October, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

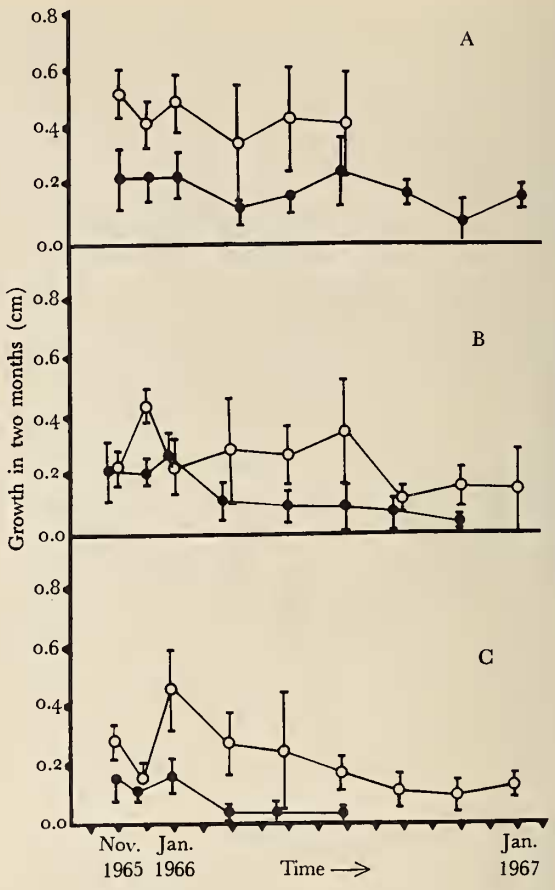

Figure 4

Growth fluctuations for mussels set in cages at Santa Barbara Harbor (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period October, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

ceived an extensive pounding on such occasions. Although I have shown (HARGER, 1967) that growth of *M. edulis* is inhibited by wave action, this was not demonstrated for *M. californianus* (at least for the moderate wave action at which the investigation was undertaken).

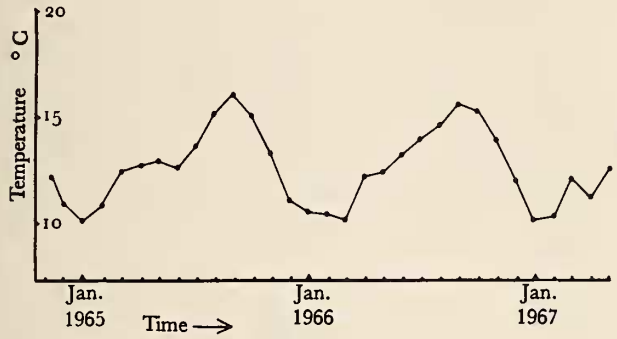

Figure 5

Mean monthly surface water temperatures from Santa Barbara Harbor. Readings were taken daily at midday.

GROWTH OF MUSSELS IN EXPERIMENTS INVOLVING "MATURE" POPULATIONS

Growth patterns of *Mytilus edulis* during both the 6 and 12 month immersion intervals were similar, this being true also for *M. californianus*. The following comments mainly concern results obtained from the 12 month interval with the understanding that no differences of importance are apparent between the 2 sets of data (more growth was of course recorded for the longer interval).

Results obtained from populations which were permitted to grow undisturbed for 12 months indicate that *Mytilus edulis* and *M. californianus* possess different growth characteristics. Figures 6 and 7 show growth curves for both species from the top and bottom intertidal positions. These curves were constructed by sorting all the mussels (each species separately) alive at the end of the 12 month period into 1 cm size classes based on the measurements made at the beginning of the experiment. The mean growth increment was then calculated for each group, and a cumulative growth curve based on the year's growth for each individual size class was then made up. For convenience, it was assumed that the mean size of any group at the start of the year corresponded to the mid point of each size class, *i. e.*, for the class 2 - 3 cm this would be 2½ cm. The resulting curve indicates the expected growth pattern the mussels would show over a number of years if all years corresponded in weather conditions, etc., to that in which the measurements were made. The data from which the curves were constructed are recorded in Tables 1 and 2 (Appendix).

Since mussels from all the different treatments have been grouped together to provide the data on which

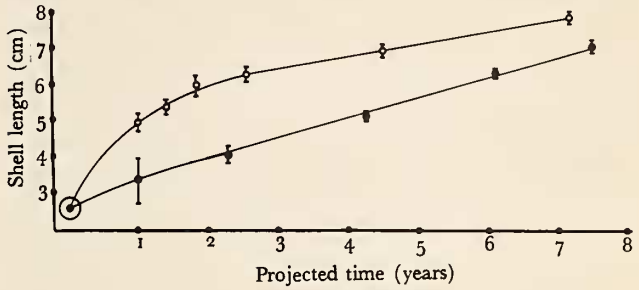

Figure 6

Projected growth curves for *Mytilus edulis* (open symbols) and *Mytilus californianus* (closed symbols), based on data obtained from undisturbed populations of mussels at the top position, Ellwood Pier (see text). Growth occurred between August, 1965 and August, 1966. Twice the standard error of the mean for each size class (see text) is represented by a bar on each side of the symbol. (Data used to construct these curves may be found in Table 1 in the Appendix.)

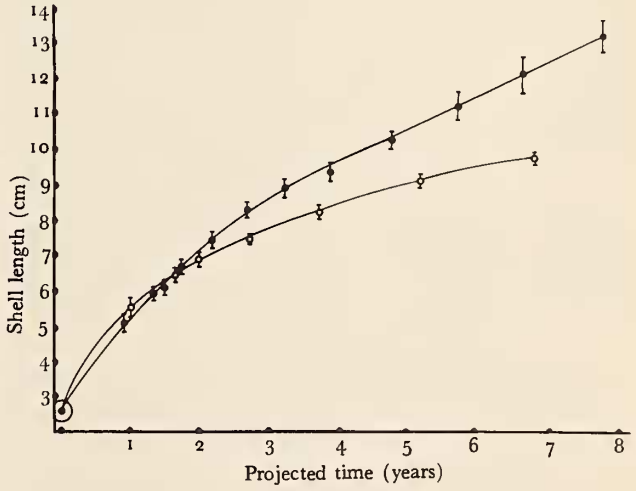

Figure 7

Projected growth curves for *Mytilus edulis* (open symbols) and *Mytilus californianus* (closed symbols), based on data obtained from undisturbed populations of mussels at the bottom position, Ellwood Pier (see text). Growth occurred between August, 1965 and August, 1966. Twice the standard error of the mean for each size class (see text) is represented by a bar on each side of the symbol. (Data used to construct these curves may be found in Table 2 in the Appendix.)

these curves are based it is probable that these results are representative of the growth that would occur in heterogeneous natural populations.

At the lowest level *Mytilus edulis* grew slightly more than *M. californianus* for approximately the first year, *i. e.*, until *M. edulis* reached a length of 5 - 5½ cm; thereafter, growth of *M. edulis* fell off and almost ceased by the time the mussels had reached a length of 10 cm or so. Growth of *M. californianus* did not fall off appreciably until individuals had reached at least 15 cm (2 to 3 years). Growth rate exceeded that of *M. edulis* increasingly after a length of about 6 cm had been reached. At the high level, growth of *M. edulis* of all sizes was always exceeded by that of *M. californianus*.

The curves for mussels growing in the low posititon are similar to those recorded by Coe (1945) at La Jolla, California, except that considerably higher growth for both *Mytilus edulis* and *M. californianus* was obtained at La Jolla than at Santa Barbara. This, overlooking the possible effects of temperature and differing geographical conditions, was most probably due to the difference in culture techniques. Coe's technique consisted in keeping mussels submerged and out on wire trays; this obviously avoids any effects of intraspecific competition and so maximum growth would be recorded. An effect such as this is apparent when growth of mussels from the disturbed populations (those used to obtain seasonal fluctuations) is compared with growth from the long term undisturbed populations. For instance, the 3 to 4 cm size class for *M. californianus* growing in the bottom cages at Ellwood Pier showed a mean annual increase of 3.08 cm ±0.48 cm for the disturbed cages and 2.33 cm ± 0.12 cm for the undisturbed cages. A similar trend is present in the other sizes and is also to be found in *M. edulis*. This difference presumably arose because of effects of intraspecific and interspecific competition were continually reduced in the disturbed populations by the bi-monthly inspections which served to rearrange mussels.

THE EFFECT OF INTERTIDAL EXPOSURE ON GROWTH OF *Mytilus edulis* AND *Mytilus californianus*

Cages were set out at top, middle, and bottom intertidal positions for the 6 month period only. Discussion of the effects of intertidal position on growth will therefore be confined mainly to data obtained during this time interval.

Because small mussels exhibit a growth pattern which differs from that of large mussels, each population has been divided into 2 groups. The first is comprised of all those mussels originally smaller than 4 cm, and the second, those larger than 5 cm. Mussels between 4 and 5 cm are not included in order that a clear distinction between the growth patterns exhibited by small and large mussels can be made.

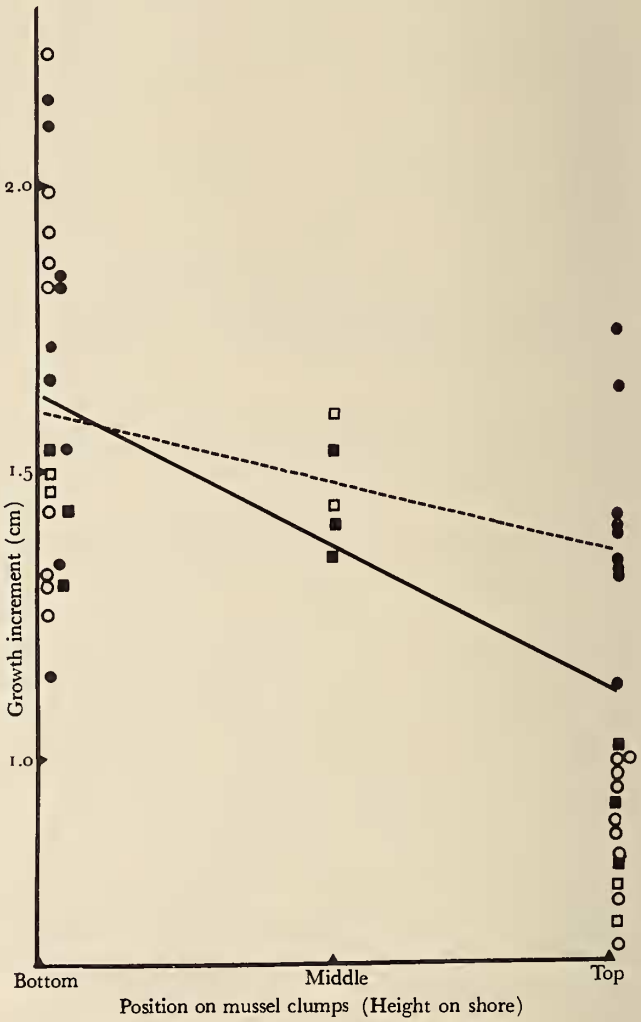

Figure 8

Mean growth increment per cage for mussels initially under 4 cm in length, plotted against height of cage (*i. e.*, height on shore). The mussels were allowed to grow undisturbed for 6 months (August, 1965 to February, 1966). ○ represent *Mytilus edulis* from cages in which both species occurred. □ represent *Mytilus edulis* from pure clumps. ● represent *Mytilus californianus* from mixed clumps and ■ represent *Mytilus californianus* from pure clumps. *Mytilus californianus* is represented by the dashed regression line and *Mytilus edulis* by the solid line. The regression coefficients for the two lines are significantly different from each other ($P < 0.001$), see Table 3.

(a) Mussels Initially Under 4 cm

Growth of smaller mussels is shown in Figure 8. Here, mean growth increment for each cage has been plotted against height on shore. There was no significant difference between the growth of the 2 species at the lower or middle positions, but the growth of *Mytilus edulis* in the top position was markedly lower than that of *M. californianus* (Table 2). The slopes of the regression lines which relate height on pilings to growth increment are significantly different from one another (Table 3), which suggests that with increasing tidal exposure time growth of smaller *M. edulis* individuals is inhibited to a greater extent than is that of *M. californianus*.

Table 2

Comparison between the growth increment of small individuals of *Mytilus edulis* and *Mytilus californianus* contained within adult populations in upper cages at Ellwood Pier for the period August, 1965 to February, 1966. All measurements were obtained from mussels initially between 2.5 cm and 4.0 cm in length. (In this and following Tables 3 asterisks {***} indicate a significant difference, $p < 0.001$)

Group	M	SD	SS	F. 1,340
Mytilus edulis	0.83	0.43	166	
Mytilus californianus	1.23	0.64	176	46.66***

M = mean; SD = standard deviation; SS = sample size

Table 3

Comparison between the slopes of the regression lines relating growth increment of *Mytilus edulis* and *Mytilus californianus* individuals initially less than 4 cm in length, growing within adult populations at Ellwood Pier, to intertidal level. The dependent variable is growth increment and the independent variable is intertidal level (top, middle, bottom positions, see text). Growth occurred between August, 1965 and February, 1966. All measurements were in centimeters

Group	SS	Regression equation	Sl	F 1,814
Mytilus edulis	371	$y = 1.64 - 0.133X$	−0.133	
Mytilus californianus	447	$y = 1.60 - 0.063X$	−0.063	15.67***

SS = sample size; Sl = slope

(b) Mussels Initially Over 5 cm

Results obtained from larger mussels are quite clear. First, growth of *Mytilus edulis* at all 3 heights is signifi-

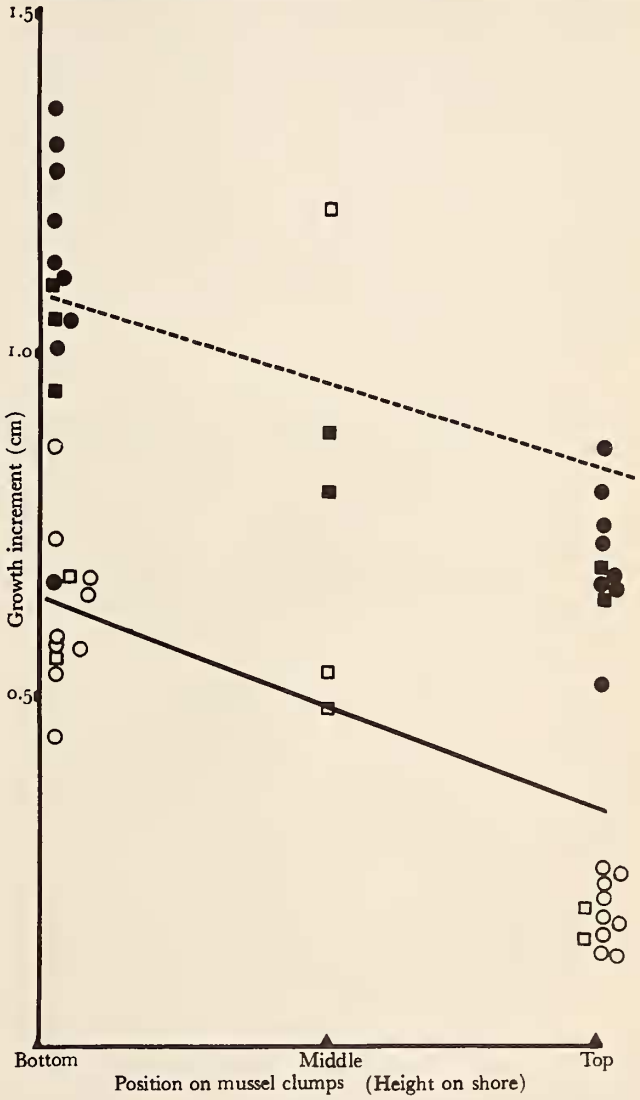

Figure 9

Mean growth increment per cage for mussels initially over 5 cm in length, plotted against height of cage (*i. e.*, height on shore). The mussels were allowed to grow undisturbed for 6 months (August, 1965 to February, 1966). ○ represent *Mytilus edulis* from cages in which both species occurred. □ represent *Mytilus edulis* from pure clumps. ● represent *Mytilus californianus* from mixed clumps and ■ represent *Mytilus californianus* from pure clumps. *Mytilus californianus* is represented by the dashed regression line and *Mytilus edulis* by the solid line. The lines are not significantly different from each other in slope, but are so in position (y intercept), $p < 0.001$.

cantly less than that of *M. californianus* (Figure 9). Figure 9 shows that for large individuals growth of both species is adversely affected to the same degree by the increased exposure associated with increased height on the shore (this was not the case for the smaller mussels).

Cages left suspended in place for one year yielded similar growth results to those reported for the 6 month period. For the smaller mussels (originally 4 cm and less), the overall relationship between the 2 species remained as before, *i. e.,* there was no significant difference between the growth of either species in cages set at the bottom level, but as before, the growth of *Mytilus edulis* in the top cages was far less than that for *M. californianus.* One difference from the 6 months' growth was that over a year's time *M. californianus* grew as much at the upper as at the lower levels.

GROWTH CHARACTERISTICS OF MATURE POPULATIONS OF MUSSELS IN SANTA BARBARA HARBOR

When both species were grown in Santa Barbara Harbor for 12 months, growth of *Mytilus edulis* was greater than that of *M. californianus* for both small and large mussels (Figure 10).

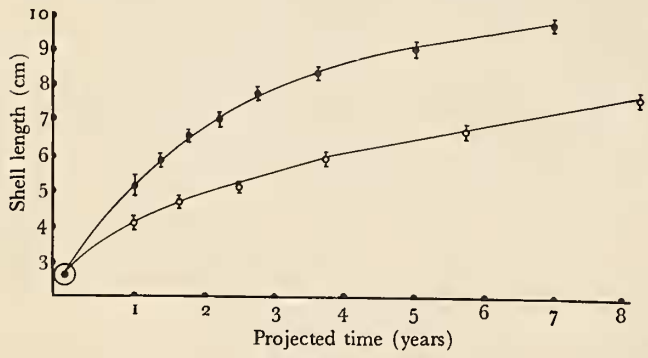

Figure 10

Projected growth curves for *Mytilus edulis* (open symbols) and *Mytilus californianus* (closed symbols), based on data obtained from undisturbed populations of mussels at Santa Barbara Harbor. Growth occurred between August, 1965 and August, 1966. Twice the standard error of the mean for each size class (see text) is represented by a bar on each side of the symbol. (Data used to construct these curves may be found in Table 3 in the appendix.)

COMPARISON BETWEEN GROWTH CHARACTERISTICS OF MATURE POPULATIONS AT ELLWOOD PIER AND SANTA BARBARA HARBOR

Growth of smaller mussels (2 - 4 cm) from mature pure species populations in the harbor, when compared with that of mussels from similar treatments at the low positions on the Pier indicated that *Mytilus californianus* populations at the Pier grew faster than those in the harbor; no significant difference could be detected between the *M. edulis* populations from the two locations. Larger *M. edulis* at the Pier, however, grew at a faster rate than those in the harbor (Table 4). After *M. edulis* has reached 6 - 7 cm (2 to 2½ years) in the harbor, growth rate falls off markedly (Figure 10). (The data used to construct these curves are recorded in Table 3, Appendix.)

Table 4

Itemized comparison of the growth increment shown by small size classes (part of adult populations) of *Mytilus edulis* at Santa Barbara Harbor (calm water) and at the bottom position (see text), Ellwood Pier (rough water). Populations were immersed from August, 1965 to February, 1966

SC	SS	MGI	SD
SANTA BARBARA HARBOR			
2 - 3 cm	13	2.41	0.48
> 3 - 4 cm	62	1.82	0.69
> 4 - 5 cm	38	1.49	0.75
> 5 - 6 cm	40	0.72	0.59
ELLWOOD PIER			
2 - 3 cm	15	2.99	0.60
> 3 - 4 cm	98	2.44	0.62
> 4 - 5 cm	85	1.91	0.77
> 5 - 6 cm	92	1.35	0.61

Note: larger size classes (> 4 cm) exhibit a greater increase at Ellwood Pier than at Santa Barbara Harbor.

SC = size class; SS = sample size; MGI < mean growth increment; SD = standard deviation

An equivalent decrease in growth rate occurs at the Pier when a length of between 9 and 10 cm has been reached (perhaps 6 years old) (Figure 6). (The maximum size reached by natural populations of *M. edulis* in the harbor appears to be around 6 cm, whereas 8 - 9 cm is quite common for mature mussels at the Pier.

In the harbor, *Mytilus edulis* maintains a higher growth rate than *M. californianus* until it reaches a length of about 6 cm at about 2 to 2½ years of age (Figure 10); after this the rate drops and becomes less than that of *M. californianus* of equivalent size. At Ellwood Pier, the growth of *M. edulis* exceeds that of *M. californianus* until a length of 5 cm is reached after 1 year (Figure 6). (It must, however, be remembered that *M. californianus* does not normally occur in harbors.)

SUMMARY OF GROWTH CHARACTERISTICS OF MATURE MUSSEL POPULATIONS

(1) At Ellwood Pier (rough water), populations of *Mytilus californianus* grew faster than those of *M. edulis* (although at low intertidal levels small individuals of *M. edulis* grow faster than *M. californianus* of equivalent size).
(2) In Santa Barbara Harbor (quiet water), *Mytilus edulis* populations showed more growth than *M. californianus* populations.
(3) Growth of both species is reduced at high intertidal levels from that shown at low intertidal levels. Growth of small individuals of *Mytilus edulis* decreases much more sharply from low to high intertidal levels than that of *M. californianus*. Growth of large mussels of both species is reduced by the same degree from low to high intertidal levels.
(4) The greatest overall growth for both species occurred at Ellwood Pier.

GROWTH PATTERNS OF MUSSELS OBTAINED FROM COMPETITION EXPERIMENTS INVOLVING JUVENILES

(A) Ellwood Pier

At the first inspection of the experiment set in September, 1965 it was discovered that most *Mytilus edulis* individuals in the mixed species cages had crawled to the outside of the mussel clumps.

From Figure 11 it can be seen that initially the growth rate of small *Mytilus edulis* (as estimated by the slopes of the lines connecting the means) is greater than that of small *M. californianus*. This relationship holds for the first 6 to 7 months only, until *M. edulis* has reached a mean length of between 4½ and 5 cm, and *M. californianus* has reached about 3½ cm. Thereafter the growth rate of *M. californianus* is greater.

Although all treatments should have originated with mussels of a similar size, the initial (October, 1965)

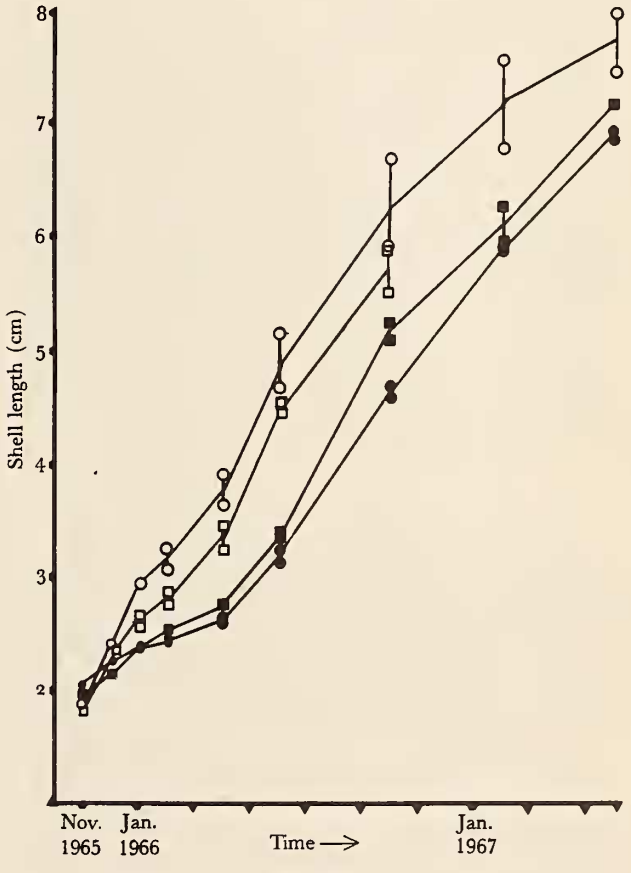

Figure 11

Progressive growth of juvenile mussels from cages set at the bottom position at Ellwood Pier (see text)
The mean length of *Mytilus edulis* growing in cages containing *Mytilus californianus* is represented by ○ and from cages containing *Mytilus edulis* only by □. *Mytilus californianus* from mixed clumps is represented by ● and from pure clumps by ■. Each symbol represents the mean length of the mussels in one cage.
From December, 1965 the mean length of the *Mytilus edulis* populations is always significantly greater ($p < 0.001$) than the *Mytilus californianus* populations. From January, 1966 *Mytilus edulis* growing with *Mytilus californianus* are larger than *Mytilus edulis* growing by themselves ($p < 0.001$). From April, 1966 *Mytilus californianus* growing by themselves are larger than *Mytilus californianus* growing in conjunction with *Mytilus edulis* ($p < 0.05$).

Mytilus edulis populations were significantly smaller than the *M. californianus* populations. After one month's growth, however, all the *M. edulis* populations, taken together, were significantly larger than the *M. californianus* populations ($P < 0.001$).

Populations of juvenile mussels first set out at Ellwood Pier during January, 1966 showed the same trends as outlined for those initiated in September, 1965.

(B) Santa Barbara Harbor

Within the experiment started in January, 1966 growth of the *Mytilus edulis* populations was at all times greater than that of *M. californianus*. For the first 4 months the populations of *M. edulis* in the harbor grew faster than those at the Pier (Table 5). During this time the growth of *M. californianus* was also greater in the harbor than at Ellwood Pier (Table 6). This relationship was reversed for both species by the end of the second 4-month period (Tables 7 and 8), *i. e.*, growth was greater at Ellwood Pier than at the harbor. During this second period large numbers of *M. edulis* recruits settled within the harbor cages and their presence undoubtedly influenced the growth of the resident mussels.

Table 5

Comparison between populations of juvenile *Mytilus edulis* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). Populations were initially not significantly different from each other in mean length of individuals. Growth occurred between 25 January, 1966 and 22 May, 1966. All measurements were made in centimeters

Group	M	SD	SS	F. 1,551
Santa Barbara Harbor	3.91	0.62	225	
Ellwood Pier	3.29	0.53	328	158.18***

M = mean; SD = standard deviation; SS = sample size

As previously stated, the harbor seas are normally quite calm; this apparently allows silt, detritus, and fecal matter to settle inside mussel clumps growing there. Such deposits accumulate and form a glutinous mud core inside clumps (Harger, 1968), often smothering centrally located mussels. Mortality due to this mechanism after one year resulted in 31/200 and 7/100 *Mytilus californianus* individuals surviving in the pure and mixed cages. The survival of *M. edulis* was 117/200 and 65/100 from the pure and mixed cages, respectively. Over a similar time interval there was no significant difference in survival of the 2 species in cages set at the low position at Ellwood Pier. Presumably this was because constant wave action at that location tended to wash any accumulating silt out of the clumps. In fact, the amount of silt accumulating in cages set at the pier was negligible (Harger, 1968).

If one compares growth of juvenile mussels from "mature" undisturbed populations with those which developed initially within "juvenile populations" (Figures 7 and 11) over a period of one year it can be seen that growth is greater among the latter mussels. This seems to be due to 2 factors: first the periodic disturbances (measuring, etc.) experienced by the juvenile populations

Table 6

Comparison between populations of juvenile *Mytilus californianus* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). Populations were initially not significantly different from each other in mean length of individuals. Growth occurred between 25 January, 1966 and 22 May, 1966. All measurements were made in centimeters

Group	M	SD	SS	F. 1,665
Santa Barbara Harbor	2.99	0.58	207	
Ellwood Pier	2.53	0.46	460	122.51***

M = mean; SD = standard deviation; SS = sample size

Table 7

Comparison between populations of juvenile *Mytilus edulis* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). These populations were initially placed in the water during 25 January, 1966, at which time there was no difference in mean length of individuals comprising them. After a period of four months' immersion (22 May, 1966), the populations in the harbor yielded individuals of a larger mean size than at the Pier (see Table 5); this difference was reversed after a further four months' growth (19 September, 1966). All measurements were made in centimeters

Group	M	SD	SS	F. 1,494
Santa Barbara Harbor	4.83	0.78	212	
Ellwood Pier	5.24	0.88	284	29.66***

M = mean; SD = standard deviation; SS = sample size

Table 8

Comparison between populations of juvenile *Mytilus californianus* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). These populations were initially placed in the water during 25 January, 1966, at which time there was no difference in mean length of individuals comprising them. After a period of four months' immersion (22 May, 1966), the populations in the harbor yielded individuals of a larger mean size than at the Pier (see Table 6); this difference was reversed after a further four months' growth (19 September, 1966). All measurements were made in centimeters

Group	M	SD	SS	F 1,486
Santa Barbara Harbor	3.69	0.64	75	
Ellwood Pier	4.11	0.88	413	15.46***

M = mean; SD = standard deviation; SS = sample size

leading to the release of oppressed individuals with subsequent growth promotion; second, perhaps some form of growth inhibition being imposed upon juveniles through competition with adults. Both probably play some part since growth of juveniles from mature but disturbed populations (see text previously) was found to be greater than that from undisturbed mature populations, but less than that of the disturbed juvenile populations.

Over long time periods (6 months to one year), when the artificial growth curves (prepared from growth increment data obtained from mussels grown without disturbance for one year) from the harbor are compared with those from the low pier position it is apparent that both species grow at a lower rate within the harbor. The growth curve for *Mytilus californianus* in the harbor (compare with Pier) is markedly depressed and is entirely below that of *M. edulis*.

CONCLUSION

The almost exclusive domain of *Mytilus edulis*, harbors and estuaries, does not seem to be the place where it is able to grow best. The crawling behavior of *M. edulis* probably insures that most *M. californianus* juveniles will be eliminated from a mixed species clump in quiet locations since silt will tend to accumulate and smother the inside mussels, which will always be *M. californianus* in such situations. In disturbed situations, however, continual wave action insures that suffocation of *M. californianus* by silt in the presence of *M. edulis* does not take place. Here the greater growth capacity of *M. californianus* enables these animals to push themselves clear of *M. edulis* in mixed species clumps. The smaller *M. edulis* are then usually incorporated within the clump matrix and crushed by their stronger competitors.

ACKNOWLEDGMENTS

This work forms part of a Ph. D. dissertation submitted at the University of California at Santa Barbara wherein all data not reported directly in this paper can be found. I wish to thank Dr. Joseph H. Connell for guidance and criticism. Additionally I owe much to Dr. D. E. Landenberger and Dr. J. Stimson for their constant criticism. Finally I wish to acknowledge the use of shore line facilities belonging to Signal Oil and Gas Company at Ellwood, without which, in view of current population densities in Southern California, this research could not have been undertaken.

LITERATURE CITED

Coe, Wesley Roswell

1945. Nutrition and growth of the California Bay-Mussel (*Mytilus edulis diegensis*). Journ. Exp. Zool. 99: 1 - 14

Coe, Wesley Roswell & Dennis L. Fox

1942. Biology of the California Sea-Mussel (*Mytilus californianus*). Journ. Exp. Biol. 90: 1 - 30

DeBach, Paul

1966. The competitive displacement and coexistence principles. Ann. Rev. Ent. 11: 183 - 212

Hardin, Garrett H.

1960. The competitive exclusion principle. Science 131: 1292 - 1297

Harger, John R. E.

1967. Population studies on *Mytilus* communities. Ph. D. Dissert., Univ. Calif. Santa Barbara; Univ. Microfilms No. 69-1719

1968. The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus* The Veliger 11 (1): 45 - 49; 3 text figs. (1 July 1968)

Soot-Ryen, Tron

1955. A report on the family Mytilidae (Pelecypoda). Allan Hancock Pacific Expeditions, vol. 20, no. 1 (Univ. S. Calif. Press, Los Angeles), 175 pp., 10 plts., 78 text figs. (10 November 1955)

Stubbings, H. G.

1954. Biology of the common mussel in relation to fouling problems. Research, London 7: 222 - 229.

APPENDIX

Table 1

Growth increment data for 1 cm size classes (original measurements) for *Mytilus edulis* and *Mytilus californianus* after one year's development (August, 1965 to August, 1966) at the top position (see text) at Ellwood Pier. These data were used to construct the curves in Figure 6

SC	SS	MGI	SE
Mytilus edulis			
2 - 3 cm	26	1.60	0.10
< 3 - 4 cm	65	1.17	0.08
< 4 - 5 cm	85	0.67	0.05
< 5 - 6 cm	78	0.43	0.03
< 6 - 7 cm	62	0.23	0.03
< 7 - 8 cm	27	0.20	0.05
< 8 - 9 cm	10	0.07	0.02
< 9 - 10 cm	15	0.05	0.02
Mytilus californianus			
2 - 3 cm	17	2.55	0.15
< 3 - 4 cm	93	2.33	0.06
< 4 - 5 cm	94	1.98	0.06
< 5 - 6 cm	85	1.51	0.06
< 6 - 7 cm	62	1.24	0.06
< 7 - 8 cm	45	0.86	0.07
< 8 - 9 cm	15	0.51	0.08
< 9 - 10 cm	17	0.29	0.07

SC = size class; SS = sample size; MGI = mean growth increment; SE = standard error of mean

Table 2

Growth increment data for 1 cm size classes (original measurements) for *Mytilus edulis* and *Mytilus californianus* after one year's development (August, 1965 to August, 1966) at the bottom position (see text) at Ellwood Pier. These data were used to construct the curves in Figure 7

SC	SS	MGI	SE
Mytilus edulis			
2 - 3 cm	15	2.99	0.16
< 3 - 4 cm	98	2.45	0.06
< 4 - 5 cm	85	1.92	0.08
< 5 - 6 cm	92	1.35	0.06
< 6 - 7 cm	61	0.94	0.05
< 7 - 8 cm	31	0.74	0.08
< 8 - 9 cm	22	0.63	0.07
< 9 - 10 cm	18	0.30	0.05
Mytilus californianus			
2 - 3 cm	19	2.70	0.16
< 3 - 4 cm	100	2.66	0.08
< 4 - 5 cm	90	2.27	0.09
< 5 - 6 cm	89	1.99	0.09
< 6 - 7 cm	65	1.86	0.09
< 7 - 8 cm	43	1.48	0.12
< 8 - 9 cm	24	0.85	0.12
< 9 - 10 cm	18	0.72	0.09

SC = size class; SS = sample size; MGI = mean growth increment; SE = standard error of mean

Table 3

Growth increment data for 1 cm size classes (original measurements) for *Mytilus edulis* and *Mytilus californianus* after one year's development (August, 1965 to August, 1966) in Santa Barbara Harbor. These data were used to construct the curves in Figure 10

SC	SS	MGI	SE
Mytilus edulis			
2 - 3 cm	13	2.42	0.13
< 3 - 4 cm	62	1.82	0.09
< 4 - 5 cm	38	1.49	0.12
< 5 - 6 cm	40	0.73	0.09
< 6 - 7 cm	30	0.47	0.07
< 7 - 8 cm	20	0.38	0.06
< 8 - 9 cm	11	0.26	0.08
< 9 - 10 cm	9	0.11	0.02
Mytilus californianus			
2 - 3 cm	4	0.85	0.30
< 3 - 4 cm	34	0.52	0.07
< 4 - 5 cm	48	0.58	0.08
< 5 - 6 cm	46	0.83	0.07
< 6 - 7 cm	40	0.57	0.06
< 7 - 8 cm	26	0.55	0.08
< 8 - 9 cm	12	0.58	0.09
< 9 - 10 cm	11	0.34	0.07

SC = size class; SS = sample size; MGI = mean growth increment; SE = standard error of mean